

Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground

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Little is known about how small-scale variation in neighbor biomass can influence the strength of root competition experienced by an individual plant. In this study, modified root exclusion tubes were used to vary the accessibility of the soil space surrounding *Amaranthus retroflexus* target plants to the neighboring plants. A gradient of root accessibility was created by drilling varying numbers of holes into standard root exclusion tubes, made of 15 cm diameter PVC pipe. Belowground competitive intensity, defined as biomass reduction due to root interactions alone, relative to growth in the absence of neighbors, was then measured along the resulting gradient of neighbor root densities. At low neighbor root abundances the strength of belowground competition was proportional to neighbor root biomass, consistent with prior evidence that belowground competition is symmetric. If belowground competition were asymmetric, neighbor roots should have had little effect on target plants when they are rare relative to those of the target plant. At higher neighbor root abundances, belowground competitive intensity should increase rapidly. The strong relationship found between neighbor root biomass and belowground competitive intensity suggests relatively small variations in root biomass could lead to large variations in belowground competition. Reduced belowground competition in areas with low root biomass could have important implications for the establishment and growth of poor belowground competitors, suggesting a mechanism by which species coexistence may occur despite extremely intense root competition.

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Competition for belowground resources can be intense in natural communities, often limiting plant growth and establishment (Casper and Jackson 1997). In field studies, root competition is often measured as either the proportional growth reduction of a target plant due to root interactions with its neighbors compared to growth with no neighbors (Wilson and Tilman 1991, 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998), or as proportional growth when competing belowground with neighbors (Cahill 1999). Regardless of the methods used to calculate the strength of root competition, several prior

studies show there exists substantial variation in the strength of belowground competition within a community (Belcher et al. 1995, Peltzer et al. 1998, Cahill 1999). For example, in a low diversity grassland, the coefficient of variation (CV) associated with the mean strength of root competition can exceed 100% (Peltzer et al. 1998). Cahill (1999) found similarly high variation in the strength of root competition within a relatively small area (0.25 ha) in fertilized plots in an early successional field. In a low-biomass wetland, the CV associated with the mean strength of belowground competition was in excess of 200% (Twolan-Strutt and

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Keddy 1996). Such high degrees of variability in root competition within relatively small areas suggest local processes, such as local variation in root density or soil resource availability may be at least as important in determining individual plant growth as are the more commonly studied landscape scale patterns of how the mean strength of competition can vary with productivity (Wilson and Tilman 1991, 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999).

Here we explore whether local variation in neighbor root abundance could cause the high degree of variation in the strength of belowground competition commonly observed. If this hypothesis is correct, we would expect to find a strong correlation between the strength of root competition and the amount of neighbor roots with which an individual plant can interact. Surprisingly, this relationship has not been previously examined in the field, although several studies have examined correlations between aboveground neighbor biomass and belowground competition (Wilson and Tilman 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Cahill 1997, Peltzer et al. 1998). At a most basic level, information directly assessing the relationship between neighbor root biomass and the strength of root competition in the field is lacking.

By determining the form of the relationship between neighbor root biomass and the strength of root competition we can also evaluate the prediction that belowground competition is size-symmetric (Wilson 1988, Gerry and Wilson 1995, Weiner et al. 1997). Symmetric competition results when individuals compete in proportion to their size, with large plants causing a large decrease in the growth of smaller plants, and small plants causing a small (but proportionate to their size) decrease in the growth of the larger plant (Weiner et al. 1997, Schwinning and Weiner 1998). In contrast, aboveground competition is generally size-asymmetric (Harper 1977, Weiner 1985, Weiner and Thomas 1986), because large plants disproportionately reduce the amount of light reaching smaller plants, while the smaller plants have little or no effect on the light reaching the larger plant. Determining the symmetry of root competition in the field is essential to understanding the nature and effects of belowground interactions in natural communities, as symmetric and asymmetric competition can differentially affect population dynamics (Schwinning and Fox 1995, Schwinning 1996), and community composition (Newman 1973, Cahill 1999).

Root competition is hypothesized to be size-symmetric (*sensu* Schwinning and Weiner 1998) because nutrient uptake appears to be proportional to the size of a plant's root system (Wilson 1988, Gerry and Wilson 1995, Weiner et al. 1997). Root competition between neighboring plants occurs when depletion zones, created by resource uptake by the roots, spatially overlap (Baldwin 1976, Caldwell and Richards 1986). The ex-

perimental support for symmetric competition below ground comes from two greenhouse studies (Wilson 1988, Weiner et al. 1997) and just one field study (Gerry and Wilson 1995). Since it is unclear to what extent results from greenhouse studies in pots can be extrapolated to natural systems, more field studies are clearly warranted.

Here we report the findings of a field experiment in which we manipulated the quantity of neighbor roots interacting with target plants in order to determine whether a correlation exists between neighbor root biomass and the strength of belowground competition. The form of the observed relationship was then used to evaluate whether root competition is size-symmetric or size-asymmetric.

Methods

Study site and species description

This experiment was conducted in a 2.5-ha field within the "Laurels Preserve", located in SE Pennsylvania, USA, owned and managed by the Brandywine Conservancy. At the time of the study, the experimental field was dominated by grasses (*Dactylis glomerata* L., *Anthoxanthum odoratum* L., *Poa pratensis* L.) and Canada thistle (*Cirsium arvense* L.), with at least 45 other herbaceous species present. Non-woody root biomass averaged 735 (379) g m⁻² (S.D.) in this site (Cahill 1997). Strong belowground competition, high root biomass, and shallow rooting depth (Cahill 1997, 1999) make this site ideal for investigating the relationship between neighbor root biomass and belowground competitive intensity.

Amaranthus retroflexus L. (Amaranthaceae), red-root amaranth, was chosen as the target species because it is a common annual plant at this field site, non-clonal, and non-mycotrophic. Being non-mycotrophic is important as it allows us to modify the rooting space of the target plant without concern that we may also alter the ability of the plant to form mycorrhizae.

Experimental design

Root exclusion tubes were created from 15.25 cm diameter × 20 cm length pieces of PVC pipe. The exclusion tubes were placed vertically into the soil, in order to separate roots of a target plant that was to be planted inside the tube from the roots of naturally occurring vegetation surrounding it. More than 85% of the root biomass in this system is found within the top 20 cm (Cahill 1999), thus these exclusion tubes eliminate the majority of belowground interactions between the target plants and its neighbors. Differing quantities of neighboring roots were allowed to access the soil

within the tubes by the presence of different numbers of approximately 2-cm holes drilled through the sides of the tube prior to installation. Four of these accessibility treatments consisted of 0, 18, 36, or 72 holes; a fifth treatment used no tube at all, allowing for full root interactions between the target plant and its surrounding neighbors. These five accessibility treatments resulted in approximately 0, 12.5, 25, 50, and 100% of the total tube surface area open to neighboring roots, respectively. Tubes were installed in late February 1995. A 16 × 20-cm hole was excavated for each tube, which was then refilled with the excavated soil, minus any large rocks or woody roots.

Experimental plots (1 m²) were arranged in 14 blocks, with one replicate of each treatment per block, for a total of 70 plots. Plots were separated by at least 1.5 m, and blocks by at least 10 m. In March 1995, one 14-d-old seedling of *A. retroflexus* was bare root transplanted into the center of each exclusion tube. Following transplanting, plots were hand-watered daily for two weeks, and any individuals dying during this time were replaced. Volunteer seedlings emerging inside the tubes were removed. Within each plot, the above-ground vegetation surrounding each exclusion tube was pulled away from the target plant using thin tree netting, forcing all interactions between the target plants and the surrounding vegetation to be belowground. This method to remove aboveground interactions has been used successfully in another study at the same location, with no evidence of confounding effects on the growth of the neighbor plants (Cahill 1999).

Plant measures

Plant height and the width of the largest leaf were measured biweekly for each plant. During the course of the experiment, 45 of the initial 70 target plants experienced severe herbivory and could not be used in the final statistical analyses. We thus eliminated block as a factor in all analyses and sample sizes were uneven between treatments. The remaining 25 plants were harvested after approximately 10 weeks, when the largest plants had begun to flower. Plants were cut at the soil surface, dried for 24 h at 70°C, and weighed. To quantify neighbor root biomass, we: (1) removed the exclusion tube and soil from the ground (except for plots in which no tube was inserted, for which we dug out a similar volume of soil), (2) recovered as much of the root system of *A. retroflexus* as possible, and (3) sieved the remaining soil to remove the neighbor roots (2-mm sieve). Roots of *A. retroflexus* broken off during processing could not be separated from neighbor roots. Additionally, when the plots were initially established not all of the roots killed by installing the tubes were removed from the soil. As a result, roots retained on the sieve at harvest consisted of both old dead roots

and new live roots. Since no attempt was made to separate roots as a function of health, our measures of neighbor root biomass overestimate the actual amount of living, functional roots a target plant could interact with. In fact, measures of neighbor root biomass in the full exclusion tubes were greater than zero ($\bar{X}(SE) = 0.69(33)$ g per tube). There is no reason to believe the degree of overestimation varied among treatments, and thus reported neighbor root biomasses are relative, rather than absolute measures. All plant parts were dried at 70°C for 24 h with stolons and woody roots weighed separately from the smaller roots. Since stolon and woody roots were very rare and less likely to be directly involved in competition, they were excluded from all analyses.

Statistical analyses

To determine when belowground competition began to affect plant growth, a repeated measure MANOVA was conducted using the root accessibility treatment (fixed) and time (repeated, fixed effect) as independent variables, with plant height and the width of the largest leaf at each of the four biweekly intervals as the two dependent variables.

The effects of the root accessibility treatment on the growth of the target plants and neighbor roots were tested with two ANOVAs. In both analyses, the root accessibility treatment served as the independent variable with either $\ln(\text{target plant biomass})$ or $\ln(\text{neighbor root biomass})$ as the dependent variable. Data were transformed to satisfy the assumptions of ANOVA. All statistical analyses were conducted using SPSS 8.0 (SPSS 1997).

A testable prediction of symmetric competition

Plant growth in this field is nutrient limited, since fertilization increased plant growth (Cahill 1997, 1999). As a result, the strength of root competition can be measured as differences in biomass between plants that are competing belowground with neighbors, and control plants that are grown in the absence of competition. Belowground competitive intensity (BCI) was calculated for all plots in which neighbor roots had even limited access to the soil within the tubes:

$$BCI = \left(\frac{\bar{T}_{NN} - T_{RN}}{\bar{T}_{NN}} \right) \quad (1)$$

where \bar{T}_{NN} is the mean biomass of all target plants which had no interactions with neighbors (Mean (SD); 0.80(0.42); $n = 5$), and T_{RN} is the biomass of each of the 20 remaining target plants from the four root treatments which allowed for some degree of belowground

interaction with the neighboring plants. If neighbor roots do not reduce growth relative to control plant growth, BCI will equal 0, values between 0 and 1 are evidence of competition, and $BCI < 0$ indicates facilitation.

If belowground competition is size-symmetric, then the presence of any amount of neighbor roots should affect target plant growth in proportion to neighbor root abundance (sensu Connolly and Wayne 1996). In fact, there should be a fixed “per-gram” effect (sensu Goldberg 1990) of neighbor roots on target plant growth, with belowground competitive intensity (BCI) being directly proportional to the abundance of neighbor roots (Fig. 1). In contrast, if root competition is asymmetric, neighbor roots should have a greater per-gram competitive effect at higher neighbor root abundances (sensu Connolly and Wayne 1996). Therefore, a small quantity of neighbor roots should have little effect on target plants, as the larger target should have a disproportionate competitive advantage. Only when neighbor roots are abundant in comparison to those of target plants should there be a substantial negative effect of neighbor roots on target plant growth. As a result, BCI should be 0 or very low when neighbor roots are present at low levels, but at some level of neighbor root abundance, there will be a rapid increase in BCI with further increases in neighbor roots (Fig. 1).

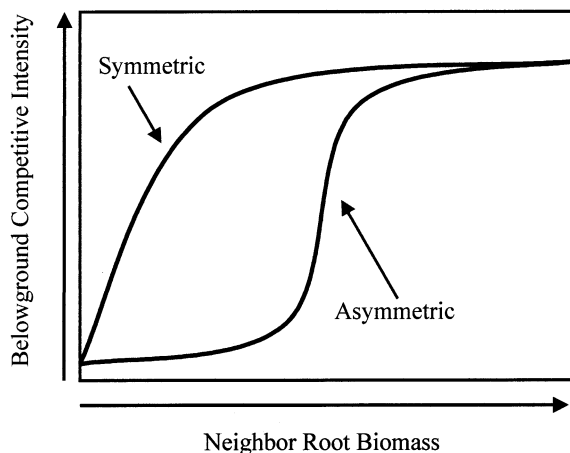


Fig. 1. Hypothetical relationship between neighbor root biomass and belowground competitive intensity as a function of the symmetry of belowground competition. If belowground competition is size-symmetric, neighbor roots should reduce target plant growth at all relative root abundances. If root competition is asymmetric, then neighbors should have no effect on target plants when the neighbors are relatively rare (low root abundance), but have a severe negative effect when common. This would be seen as an initially horizontal relationship between neighbor root biomass and target plant growth, followed by a rapid increase in the strength of root competition when neighbor roots are very abundant. Regardless of the symmetry of root competition, the curve should decelerate at high neighbor root abundances due to a diminishing effect of additional neighbor roots as target plants are likely already surrounded by neighbor depletion zones.

Our model is similar to that presented in Weiner et al. (1997); however, they differ in several important details. (1) We use belowground competitive intensity as a response variable while Weiner et al. (1997) used growth rate. (2) We are specifically investigating the relationship between the size of a neighbor’s competing organs (roots) and the strength of root competition, as opposed to the relationship between the strength of root competition and the size of the entire neighbor plant (or age; Gerry and Wilson 1995, Weiner et al. 1997). (3) We allow for a decrease in the per-gram effect of neighbor roots at high neighbor root abundances, regardless of the symmetry of competition. If in fact belowground competition occurs through overlapping depletion zones around roots, there should be a point when further increases in neighbor root biomass would not result in greater depletion zone overlap and therefore have little additional effect on target plant growth (Casper and Jackson 1997). Thus at high root biomass, there will be a gradual decrease in the slope of the relationship as neighbor root biomass increases (Fig. 1). If root competition is symmetric, the best-fit curve to the empirical data would be a simple decelerating curve, described by a quadratic relationship between competition and neighbor root biomass. If asymmetric, the curve should be logistic, with two shifts in the direction of the slope, and therefore best explained by a cubic relationship. Determining which of several possible curves “best” describes the relationship between two variables is notoriously difficult, and we used both linear and nonlinear regressions.

Linear regression

To distinguish between cubic and quadratic models, a step-wise regression was used. Belowground competitive intensity served as the dependent variable, with neighbor root biomass (NRB), NRB^2 , and NRB^3 as the three independent variables added in that order. We determined whether the addition of the quadratic and cubic terms significantly improved the regression model by testing the significance of the change in the F values associated with the addition of the higher order terms. If the addition of a cubic term does not cause a significant change in the F value (compared to a quadratic model), we then would accept a quadratic relationship between the two variables, and thus symmetric competition.

Nonlinear regression

In a second approach, we used a nonlinear model previously used to distinguish between functional response curves (Marshall and Boutin 1999). Since our predicted curves resemble type II and III functional response curves, similar statistical methods are appropriate. Following the methods of Marshall and Boutin (1999) we fit a modified Michaelis-Menten equation (as presented in Messier 1994) to our data:

$$BCI_{\text{predicted}} = \frac{A(NRB)^C}{B + NRB^C} \quad (2)$$

where NRB represents the neighbor root biomass surrounding a target plant, A is the asymptote, B is the value of x when $y = A/2$, and C represents the shape of the curve. A simple decelerating curve occurs when $C = 1$, and a sigmoidal curve occurs when $C > 1$. The larger the value of C , the more “sigmoidal” the curve (Marshall and Boutin 1999). In one run of the model, we set the initial parameter values to $A = 1$ (theoretical maximum value for BCI), $B = 1$ (visual approximation), and $C = 3$ (would represent a very sigmoidal shape), and used SPSS to fit a curve estimating the values using an iterative least-squares approach. If the value of C was determined to be approximately equal to 1, then it would support the idea that root competition is symmetric, as that would represent a simple decelerating curve. If C was substantially greater than 1 the curve would be very sigmoidal and therefore it would be evidence for asymmetric competition belowground. In a second run of the model, we set $C = 1$, which results in a simple two-parameter model (decelerating curve). We used Akaike Information Criteria (AIC) (Akaike 1973, 1978) to distinguish whether the addition of the third parameter improves the fit of the model. AIC takes into consideration sample size and number of parameters upon which a model is based (Akaike 1973, 1978), and has been used in a prior study investigating the size-symmetry of competition (Stoll et al. 1994). In our study, we calculated AIC using the equation presented in Tsangridis and Filippousis (1994):

$$AIC = N \ln(S) + 2m \quad (3)$$

where N is the sample size, S is the regression sum of squares, and m is the number of parameters used in the model. The preferred model is the one with the lower AIC (Akaike 1973, Sakamoto et al. 1986, Lefebvre 1995). Although there is no significance test associated with the use of AIC, it is generally accepted that if the AIC values calculated from two models do not differ by more than two, the model with fewer parameters should be accepted (Sakamoto et al. 1986). If the two-parameter model performs as well as the three-parameter model, that would again be support for size-symmetric competition belowground.

For both the linear and non-linear regressions, neighbor root biomass was used as the independent variable in regression. While root length is a better indicator of the surface area involved in resource uptake, it is also much more difficult to measure. Since the experiment was conducted in a small, relatively homogenous area (<0.25 ha) within a larger field (>2 ha), and not along a consistent vegetation or soil resource gradient, we are confident that the rela-

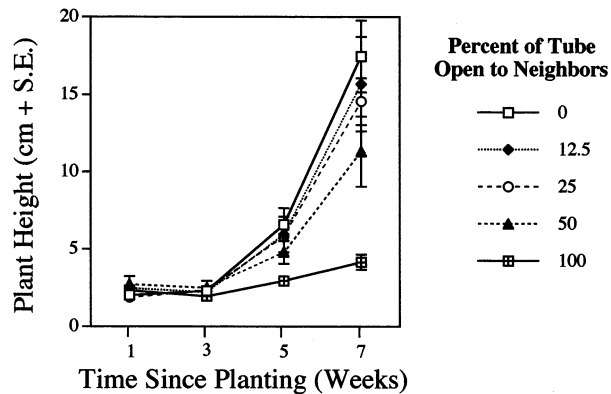


Fig. 2. Plant height \pm S.E. as a function of time since planting and root accessibility treatment. Each line represents one of the five root accessibility treatments which ranged from 0 to 100% of the tubes open to neighbor roots. The graph of leaf number versus time since planting was similar in appearance and therefore not presented.

tionship between root length and root biomass did not vary among treatments.

Results

Plant growth

Target plant growth was significantly affected by the root accessibility treatments, as can be seen from the morphological measures (Fig. 2). In a repeated measures MANOVA, belowground treatment, time since planting, and the time \times treatment interaction all significantly affected our morphological measures of plant size (height and leaf width) (Belowground Treatment: Wilk's $\Lambda_{8,88} = 0.637$, $p < 0.01$, Time: Wilk's $\Lambda_{6,40} = 0.172$, $p < 0.0001$, Trt. \times Time: Wilk's $\Lambda_{24,140} = 0.415$, $p < 0.05$). In a planned comparison contrasting plant size when grown with no neighbor roots or with full neighbor root accessibility, there was a significant effect of root competition after only three weeks of growth ($p < 0.0001$).

By varying the number of holes in the PVC tubes we were successful in varying both the biomass of neighbor roots that were able to grow into the tubes (ANOVA: $F_{4,20} = 7.279$, $p = 0.0009$, $n = 25$; Fig. 3a) and the aboveground biomass of the target plants (ANOVA: $F_{4,20} = 6.035$, $p = 0.002$, $n = 25$; Fig. 3b). Neighbor root biomass increased and target plant biomass decreased with increasing numbers of holes in the exclusion tubes (Fig. 3). There was no relationship between neighbor root biomass and target plant root:shoot ratio ($R^2 = 0.0093$, $p = 0.647$, $n = 25$).

Symmetry of competition

Both methods of regression support the size-symmetric model of belowground competition. In the regressions of neighbor root biomass and belowground competitive intensity (BCI), linear, quadratic and cubic models were all significant, with R^2 increasing as more terms were added (Table 1). However, in stepwise regression, only the addition of the quadratic term (and not the cubic one) significantly improved the fit of the model (Table 1). Equally important is a visual observation of the data (Fig. 4). At low neighbor root biomass, small increases in root biomass were associated with large increases in the strength of root competition, as was predicted

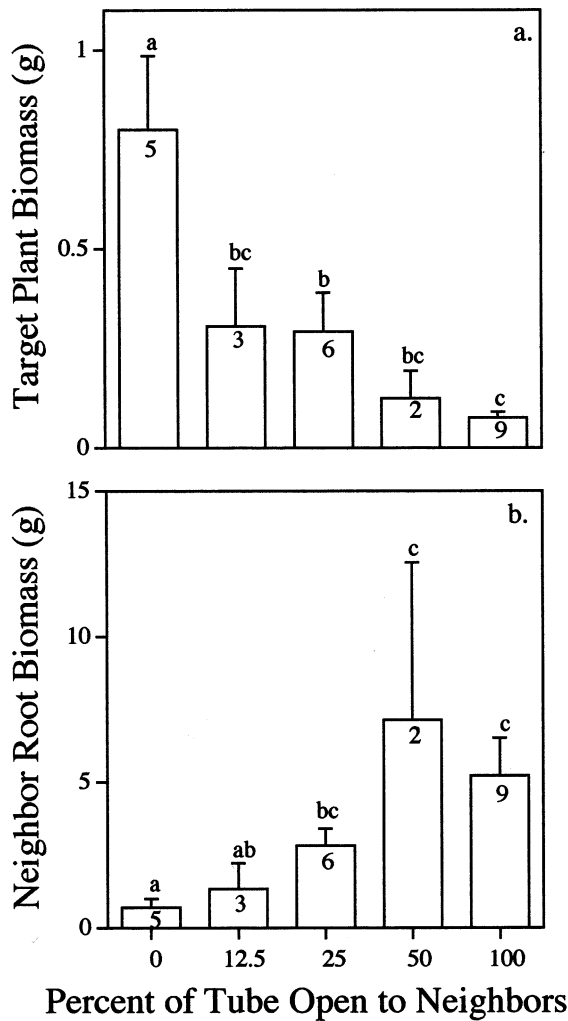


Fig. 3. a. Mean target plant biomass for each of the five root accessibility treatments. b. Mean neighbor root biomass per tube for each of the five root accessibility treatments. Error bars represent one S.E. of the mean. Within each graph, similar letters above the columns represent means that are not significantly different (SNK: $p > 0.05$). Sample sizes are given inside each of the five columns.

assuming symmetric, but not asymmetric competition belowground.

Results from the nonlinear regression support the findings from the linear regressions. When fit to the modified Michaelis-Menten equation (2), neighbor root biomass explains 54% of the variation in belowground competitive intensity (Fig. 4). More importantly, the value of the parameter C was 1.20 ± 0.54 SE (Table 2), clearly not significantly different than 1, supporting the idea that a simple decelerating curve best describes the observed relationship between neighbor root biomass and BCI. When the regression was run setting $C = 1$ (and forcing a decelerating curve), there is only a minimal change in the resulting R^2 (Change = -0.00478), or in the values of A or B in the model (Table 2), providing further evidence that a simple decelerating curve is a better fit to the data than a more complicated sigmoidal curve. The AIC for the two-parameter model was less than that of the three-parameter model (Table 2), also supporting the argument that the relationship between neighbor root biomass and competitive intensity is best explained by a decelerating, rather than sigmoidal curve.

Discussion

Variation in the strength of root competition

This study provides the first evidence in a natural system that neighbor root biomass is strongly correlated with the strength of belowground competition experienced by target plants. This strong correlation suggests that any naturally occurring variation in root biomass could explain the spatial variation in root competition commonly detected in field studies (e.g. Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999). Naturally occurring areas of low root biomass, "root gaps", may be important in allowing poor belowground competitors to persist in a system with a high mean value of belowground competitive intensity. Other experimental work also suggests root gaps can be associated with decreased competition for water (Aguilera and Lauenroth 1993, Hook et al. 1994), or soil nutrients (Cahill 1997). Spatial variation in belowground competitive intensity could be a factor in allowing poor root competitors to persist within this system. In the context of our study site, it could explain why *A. retroflexus* naturally occurs there, despite as much as a 90% reduction in growth due to root interactions, in the absence of aboveground competition (Fig. 4).

Prior attempts to find a correlation between the strength of root competition and neighbor biomass have generally focused on neighbor shoot biomass, rather than neighbor root biomass. Results have been mixed, with several finding neighbor shoot biomass to be negatively correlated with the strength of root com-

Table 1. ANOVA table for linear, quadratic, and cubic regressions analyzing the relationship between belowground competitive intensity (BCI) and neighbor root biomass. BCI refers to the proportional growth reduction experienced by target plants when interacting with neighbor roots, but not shoots, relative to mean target plant growth in the absence of any neighbor interactions. Linear, quadratic, and cubic terms were forced into the model in order, in a stepwise fashion. ANOVA results are presented after each step, including changes in F values associated with adding quadratic and cubic terms. The change in F is calculated as the difference in sums of squares between the higher and lower order models, divided by the error mean square of the higher order model. Asterisks correspond to p -values (* $p < 0.05$, ** $p < 0.01$, n.s. $p > 0.05$). Although all three models are significant, only the addition of the quadratic (and not the cubic) term significantly improved the fit of the regression model.

Regression model	DF	Regression SS	Residual SS	Error MS	F	Adj. R^2	Change in F	DF
Linear	1, 18	0.209	0.833	0.046	4.505*	0.156	—	—
Quadratic	2, 17	0.519	0.523	0.031	8.426**	0.439	10.076***	1, 17
Cubic	3, 16	0.623	0.419	0.026	7.936**	0.523	3.990 ^{n.s.}	1, 16

petition (Wilson and Tilman 1993, 1995), and others finding no relationship (Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Cahill 1997, Peltzer et al. 1998). The mixed results could be due to a variety of factors, including: (1) A correlation between shoot biomass and root competition would only be found if neighbor root biomass is tightly correlated with neighbor shoot biomass. This assumption may not be valid, as root:shoot ratios can vary along productivity gradients (Berendse and Elberse 1989, Gleeson and Tilman 1990). (2) Plants demonstrate phenotypic plasticity in response to shoot competition (e.g. Schmitt and Wulff 1993), often changing aboveground allometry (Anten and Hirose 1998, Casper et al. 1998). Plants also alter allocation to belowground structures in response to changes in soil resource availability (Gedroc et al. 1996). It is unknown whether similar allometric changes occur belowground in response to root competition. Any such changes in root allometry as a function of the strength of root competition would obscure any potential relationship between neighbor shoot biomass and root competition. (3) Some studies use mean values of shoot biomass sampled at scales larger than that experienced by individual plants, thus obscuring any relationship (e.g. Cahill 1997). (4) Alternatively, under certain conditions there actually may not be a relationship between root competition and neighbor biomass (sensu Davis et al. 1998).

The few studies examining a relationship between root biomass and competition have shown that larger root systems can confer greater overall competitive ability in the presence of both root and shoot interactions (e.g. Gaudet and Keddy 1988, Aerts et al. 1991). Jones et al. (1989) found that in a bottomland hardwood forest, focal plant growth decreased as the biomass of invading roots increased. However, they did not separate aboveground and belowground competition, and since root and shoot competition may interact to influence plant growth (Cahill 1999), it is not possible to infer the direct relationship between neighbor root biomass and belowground competition from their study.

The use of root exclusion tubes can have several undesired effects on plant growth (Casper and Jackson

1997). In particular, the number of holes drilled into the exclusion tubes may have differentially affected water drainage. Although we did not directly measure soil moisture, our results suggest this was not an important factor. Even within a single root accessibility treatment (e.g. all tubes with 36 holes) plants were smaller in those tubes with more neighbor roots than in those with fewer neighbor roots. This suggests that the abundance of neighbor roots does influence plant size, independent of any changes in soil moisture due to drainage differences. Additionally, even the largest target plants were small in comparison to the size of tubes used, thus there was no evidence that plants ever became “tube-bound”.

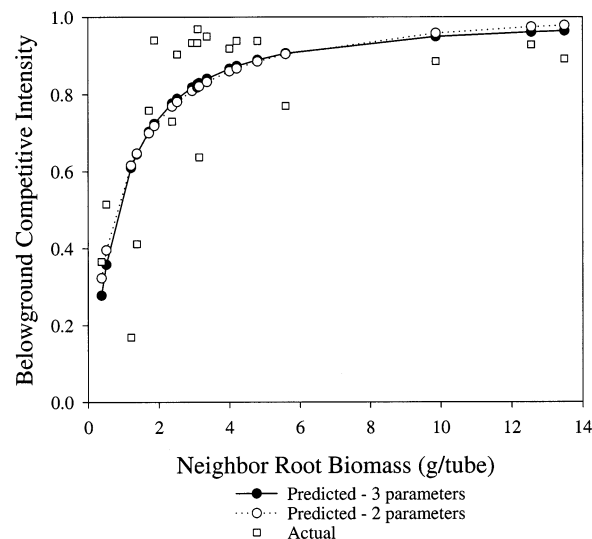


Fig. 4. Relationship between neighbor root biomass and belowground competitive intensity. Only those plots that were not disturbed by mammalian herbivores were used ($n = 25$). Two nonlinear regression lines are presented. The first was derived using a modified Michaelis-Menten equation containing three parameters. The second only used two parameters. It is visually apparent that the more complicated model did not significantly improve the fit of the curve. There is no evidence that BCI is invariant at low neighbor root abundances, and thus these data support the contention that root competition is symmetric in natural communities.

Table 2. Analysis table and solved parameter values for two nonlinear regressions analyzing the relationship between belowground competitive intensity (BCI) and neighbor root biomass. In the first analysis, a modified Michaelis-Menten equation (2) was fit to the data, with the parameters A and B determined through an iterative least-squares approach. In this analysis, the model term “ C ” was not included, forcing a simple decelerating curve as predicted under size-symmetric competition. In a second analysis, model terms A , B , and C were iteratively solved. Values of C much greater than one represent a sigmoidal curve. Akaike’s Information Criteria (AIC) were used to select the best model. AIC incorporates the number of parameter estimated, as well as the reliability of those estimates, with the model with the lower AIC preferred (Sakamoto et al. 1986).

	DF	Regression SS	Residual SS	Error MS	R^2	A (SE)	B (SE)	C (SE)	AIC
Symmetric (2 terms)	3, 17	12.555	0.483	0.028	0.536	1.039 (0.100)	0.833 (0.353)	–	54.58
Asymmetric (3 terms)	3, 17	12.560	0.478	0.028	0.541	0.998 (0.141)	0.801 (0.380)	1.200 (0.540)	56.59

Competitive symmetry

The results of both the linear and non-linear regressions are consistent with prior studies suggesting that unlike aboveground competition, belowground competition is size-symmetric. (Wilson 1988, Gerry and Wilson 1995, Weiner et al. 1997). This may reflect the fact that any increase in neighbor roots will be associated with a decrease in soil resource availability, and thus a proportional increase in the strength of root competition experienced by any individual. In the regression contrasting quadratic and cubic models, our failure to detect a significant increase in F with the addition of a cubic term (Table 1) could be due to low power, rather than the true shape of the curve (Marshall and Boutin 1999). However, the fact that both the linear and nonlinear regression methods led to the same conclusion of a simple decelerating curve greatly strengthens our contention that we observed symmetric, and not asymmetric competition belowground. Additionally, belowground competition was very strong at even the lowest ranges of neighbor root biomass (Fig. 4). If competition were asymmetric, belowground competitive intensity should have been much lower when neighbor roots were relatively less abundant.

Although the measures of neighbor root biomass were generally greater than our measures of total plant biomass (Fig. 3), this does not necessarily indicate that there were always more neighbor roots interacting with the target plant than vice versa. It is important to note that our belowground treatments ranged from excluding all root competition to allowing all root competition, even though the measures of neighbor root biomass inside the full root exclusion tubes were always greater than zero (Fig. 3). This suggests that a significant fraction of the “neighbor” roots in all treatments were dead roots which remained in the soil following tube installation, and thus measures of neighbor root biomass are overestimated. Additionally, the total amount of neighbor roots within an exclusion tube is not a direct measure of the neighbor roots functionally interacting with the target plant because competition is likely to decline with distance between roots.

Rarely discussed in the context of whether belowground competition is symmetric is the possibility that competition belowground can be through interference, rather than resource exploitation. Interference competition can occur through allelopathy, where some plants may limit the root growth of neighboring plants (Mahall and Callaway 1991, 1992). Through such interactions it may be possible for individual plants to prevent neighbors from accessing a local resource pool, and thus interference competition belowground may be more similar to competition aboveground than exploitative competition belowground. We suggest that this form of belowground competition could result in asymmetric competition.

The symmetry of competition has important implications for community structure, particularly in contributing to shifts in diversity along productivity gradients. Pronounced size hierarchies generally characterize communities in which asymmetric competition is dominant, with most of the individuals subjugated to subordinate positions (Harper 1977). As a result of these skewed size hierarchies, most of the diversity in the system is found amongst these small individuals, which are also more likely to die under intense competition (Goldberg and Miller 1990). Previous researchers (Newman 1973, Carson and Pickett 1990, Huston and DeAngelis 1994) have suggested that increased light competition should therefore result in decreased species diversity. In contrast, if symmetric belowground competition dominates, size hierarchies should be less skewed (Wyszomirski et al. 1999), and diversity should not be as severely affected by increases in competition (Newman 1973). These conceptual models thus predict a gradual decrease in diversity along a gradient of primarily symmetric competition belowground to asymmetric competition aboveground. Continued investigation into the relationship between neighbor root biomass and the strength of belowground competition, as well as further studies exploring the ecological effects of aboveground–belowground interactions may provide a better understanding of why diversity changes with productivity.

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